

Human Colonization of Asia in the Late Pleistocene

An Introduction to Supplement 17

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The origin and evolution of modern humans continues to be of great interest to the scientific and public communities alike; the field has long been dominated by findings from Europe and Africa. With new discoveries of hominin fossils and archaeological sites, in addition to the application of recent genomic and paleoclimate modeling studies, findings from Asia are serving to revolutionize the field of modern human origins. The identification of Neanderthals and Denisovans in Siberia, for example, along with growing fossil and archaeological evidence for the presence of early modern humans in East and Southeast Asia, much earlier than originally thought, places the spotlight on the evolutionary history of our species in Asia over the last 125,000 years. Exciting and unanticipated new discoveries call for a need to critically reexamine the Asian record. Taking a multidisciplinary perspective, a group of active researchers participated in a week-long Wenner-Gren symposium titled “Human Colonization of Asia in the Late Pleistocene” (#153) in March 2016. Here we review the major themes and findings emerging from the symposium and discuss avenues to move the field forward.

Background

Significant paleoanthropological findings routinely are reported from Europe and Africa owing to prolonged and large-scale research campaigns on the part of multidisciplinary teams. However, compared to these two relatively well-known regions, the Late Pleistocene record of Asia is poorly known, with fewer long-term and systematic research efforts. This is unfortunate given major paleoanthropological discoveries in Asia since the late nineteenth century by scholars such as Eugene DuBois, as well as the results of subsequent explorations in the first several decades of the twentieth century, led by scientists such as Davidson Black, Pierre Teilhard de Chardin, Wenchung Pei, Ralph von Koenigswald, Franz Weidenreich, and Hallam L. Movius (see Dennell 2001; Norton and Braun 2010). Indeed, Asia has always had major paleoanthropological potential simply due to the fact that the landmass is much larger than either Europe or Africa, and its extensive latitudinal, longitudinal, and

altitudinal breadth covers a great range of environments, including tropical forests, deserts, steppes, permafrost zones, and even open seas and oceans. Major riverways (e.g., Indus, Irrawaddy, Yangtze) connect different biomes and would have thus facilitated movement of modern humans—as recently was suggested for the European Upper Paleolithic (Hussain and Floss 2015). On the other hand, geographic barriers such as mountains and plateaus (e.g., the Himalayas, Qinling Mountain, Qinghai-Tibetan Plateau), deserts (e.g., Thar Desert, Gobi Desert), and large river systems may have served as impediments, at times, for the geographic spread of hominins, animals, and vegetative communities. During major stadials when sea levels dropped, corridors would have been created, connecting various islands to form larger landmasses in Southeast Asia; Sakhalin and Hokkaido would have been connected to mainland Siberia, and the boundary of eastern China would have extended several hundred kilometers farther east, as far as the Korean peninsula. Thus, the topography, geography, and environments of Asia were dynamic across the Late Pleistocene, acting as a canvas for the expansion, contraction, and extinction of human populations. This dynamism and diversity is reflected in Asia today, as this continent contains some 48 countries, more than 2,200 languages, and some of the highest population densities in the world.

Over the past decade or so, a plethora of new research findings in Asia and reanalyses of previously identified sites and materials have caused us to question popular models put forward to explain the origin of our species and our species' relationship to closely related ancestors (a point made in many articles in this special issue). As a consequence, the traditional

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multiregional model, where *Homo erectus* begat mid-Pleistocene *Homo*, who in turn begat modern Chinese and Aboriginal Australians (Wolpoff, Wu, and Thorne 1984; Wu and Poirier 1995), simply does not work. We now know that Neanderthals ranged much farther eastward than was previously realized (Krause et al. 2007) and that at least two other hominin populations were inhabiting eastern Asia contemporaneously, that is, the Denisovans (Reich et al. 2010) and *Homo floresiensis* (Brown et al. 2004; Sutikna et al. 2016). This is in addition to the growing evidence from genetics that demonstrates that modern humans can trace their origins to Africa (Cann, Stoneking, and Wilson 1987; Ingman et al. 2000; Jorde et al. 2000). Thus, any suggestion that the Chinese and Indonesian *H. erectus* populations lived largely in isolation and were directly ancestral to the modern Chinese and Aboriginal Australians has fallen by the wayside; instead, with so many different biological groups present in the region, it would appear the picture is a great deal more complex. Interestingly, an increasing number of studies suggest that *H. erectus* was the ancestral population of *H. floresiensis* and that that particular micropopulation likely lived largely in isolation for extended periods of time (Kaifu et al. 2011; but see Aiello 2010; Baab 2016; Martín-Torres et al. 2017; and van den Bergh et al. 2016 for further discussion and alternative hypotheses). The same case cannot yet be made for the Denisovans, although Prüfer and colleagues (2014) found evidence of gene flow from an unknown hominin into the Denisovans, hypothesizing that this archaic hominin might be *H. erectus*.

The traditional Out of Africa 2 or Replacement model to explain the origin of modern humans also has not been faring very well in recent years. There is increasing evidence that the hypothesis that proposes modern humans dispersed from Africa after 60 ka and replaced the indigenous hominin populations of Eurasia with no interbreeding (Stringer and Andrews 1988) is no longer accurate. Though early genetic studies supported the single-origin claims (e.g., Krings et al. 1997; but see Templeton 2002), whole genome studies and the retrieval of ancient DNA have now complicated this situation. A review of the plethora of genetic studies published in the past decade (e.g., Fu et al. 2015; Green et al. 2010; Prüfer et al. 2014; Skoglund and Jakobsson 2011; Stoneking and Krause 2011) indicates that interbreeding between modern humans, Neanderthals, and Denisovans occurred on at least a semiregular basis. This is not a new hypothesis, as assimilation/hybridization advocates have long made this argument based on the hominin fossil record (Smith et al. 1989, 2017; Trinkaus 2005). Furthermore, there is increasing evidence from archaeology, hominin paleontology, and geochronology that modern humans were in different areas of Asia before 60 ka, which is the date traditionally adhered to by Replacement hypothesis advocates (Bae et al. 2014; Liu et al. 2010b, 2015; Mijares et al. 2010; Norton and Jin 2009; Petraglia et al. 2007). This latter argument is consistent with the fossil finds of early modern humans in the Levant between 120–70 ka at sites like Skhul and Qafzeh (e.g., Grün and Stringer 1991; Grün et al. 2005). Indeed, the traditional Out of Africa model, which contended that modern humans rapidly

dispersed along the Indian Ocean rim using a coastal route at 60 ka (Macaulay et al. 2005; Mellars 2006b; Oppenheimer 2009) is difficult to sustain as the sole scenario explaining the peopling of Asia by our species (Groucutt et al. 2015). For example, it is possible there were multiple dispersals out of Africa where some groups initially followed the southern route while other groups of foragers took a northern route, seemingly supported by archaeology and genetic data (e.g., Di and Sanchez-Mazas 2011; Kaifu, Izuhou, and Goebel 2015; Karafet et al. 2001; Norton and Jin 2009). Further, we know from aDNA evidence that several early modern human lineages did not contribute much to the genetic makeup of later modern human populations in Eurasia, as shown by the genetic analyses of the Ust'-Ishim femur (Siberia) and the Pestera u Oase mandible (Romania; Fu et al. 2014, 2015).

Given the uncertainties of all of the present models, and in light of a great deal of new information, revised models for the origin and dispersal of *Homo sapiens* are clearly needed, with an appreciation for a more complicated demographic history and a better understanding of the timing and route(s) of dispersal across Asia. In figure 1, we illustrate the currently known spatial ranges of Neanderthals, *H. sapiens* prior to their exit from Africa, and Asian populations (Denisovans and mid-Pleistocene *Homo* as well as late-surviving(?) *H. erectus*). The Denisovan range covers only the area around the Altai where the fossils have been discovered. Modern human DNA suggests a high percentage of Denisovan ancestry in the native populations of Near Oceania and Melanesia (Reich et al. 2011); however, it is not clear whether this represents the extremities of the Denisovan geographic range or is the effect of human migrations and/or long-term isolation of these populations. The Denisovan range will likely need to be adjusted with further understanding of Denisovan population structure and distribution. Possible pathways of major *H. sapiens* dispersals from ~120–100 ka onward are shown with lines and arrows, while presumed areas of interbreeding are noted with circles and stars. For example, evidence for Neanderthal–modern human admixture events (at least two) are present in DNA obtained from the Ust'-Ishim femur as well as in the Pestera u Oase mandible, directly dated at ~45 and ~42–37 ka, respectively (Fu et al. 2014, 2015; Trinkaus et al. 2003). This is a simplistic view of processes that took place over tens of millennia and therefore should be perceived only as a rough guideline rather than a precise model. This view will evolve as our understanding of the Quaternary Asian human evolutionary record improves. Indeed, a series of recent genetics papers (e.g., Malaspinas et al. 2016; Mallick et al. 2016; Pagani et al. 2016) suggests that the figure will soon need to be revised.

Topic and Rationale

One point that is becoming increasingly clear from the analysis and reanalysis of fossil finds and excavation of archaeological sites across Asia is that a great deal of important new information is yet to be recovered, understood, and integrated into

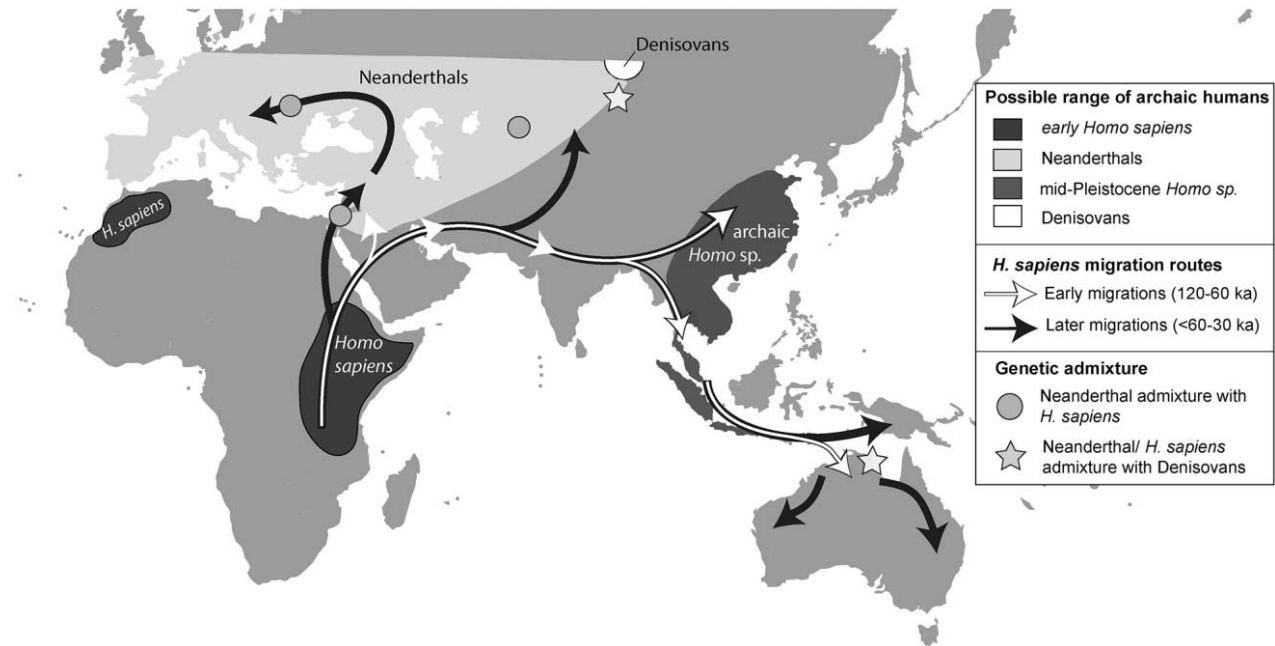


Figure 1. The various dispersal models for modern humans from Africa and into Asia. These models include proposed timings and directions of these dispersals. In addition, possible areas of geographic overlap with indigenous hominin groups (e.g., mid-Pleistocene *Homo*, *Homo neanderthalensis*) are presented with zones of likely genetic admixture between the different populations. A color version of this figure is available online.

evolutionary models. Fossil and archaeological studies, combined with newly obtained paleoenvironmental and genetic data, are contributing to a rethinking of our views about the biological and behavioral evolution of hominins in the Late Pleistocene; these revised discoveries and theories should influence the discipline for the coming decades. For these reasons, we thought that it was the right time to bring together a group of multidisciplinary experts (hominin paleontology, archaeology, geochronology, genetics) who were actively working in Asia on similar issues and questions.

In recognition of the increasing importance of the Asian record for understanding the evolutionary history of modern humans, the Wenner-Gren Foundation invited us to organize a symposium titled “Human Colonization of Asia in the Late Pleistocene.” The symposium was subsequently convened and held in March 2016 in Sintra, Portugal. The Wenner-Gren Foundation has, of course, a long and established history of organizing small, invitation-only symposia focused on topics currently being intensively debated in anthropology and related subjects. As pointed out by Leslie Aiello, then president of the foundation, human evolution was a primary focus of the organization since its inception, and many classic edited volumes focused on paleoanthropology have been published (e.g., Lee and DeVore 1968; Washburn 1961). Following on the tracks of recent paleoanthropology-focused Wenner-Gren symposia, particularly “Human Biology and the Origins of *Homo*” (Antón and Aiello 2012), our symposium continued down this path.

The three coeditors of this volume invited scholars to the symposium based on several criteria. First and foremost, participants were chosen because of their active scientific research programs in Asia across various disciplines, including hominin paleontology, archaeology, geochronology, and genetics. Second, we were also aware of the need to invite scholars from countries within Asia itself; thus participants included persons from Australia, China, Japan, and Russia. Third, we took account of gender balance, well aware of conferences that are exclusively, or almost completely, male dominated. And finally, we also thought it important to give a voice to junior and mid-level scholars, rather than hearing only from our older, venerated colleagues. Thus, the symposium held in Sintra was composed of a rather nice mix of senior- and junior-level researchers as well as male and female participants. All major regions of Asia (western and eastern, southern and northern) were covered, including both major biogeographic zones (Palearctic, Oriental). Further, we sought to cover as much longitudinal, latitudinal, and even altitudinal variability as possible. Moreover, we were able to compare mainland and island settings for contrasting views of evolutionary processes. During the week-long meeting, each participant was able to contribute a great deal of new information and be involved in discussions about the need for new models and interpretations of the Asian record. We were also delighted to see the warm and friendly interactions at the symposium, with new friendships and future collaborations formed.

The “Human Colonization of Asia in the Late Pleistocene” symposium was organized with the idea that we would be able to turn our attention to a series of questions relevant to modern human origins research from a multidisciplinary perspective. For instance, we wished to address whether modern humans initially dispersed from Africa and into Asia only once and at ca. 60 ka. Alternatively, we were interested in investigating whether there were multiple dispersals potentially predating the 60 ka event. If so, we sought to evaluate the nature of the paleoanthropological and paleoenvironmental evidence. We were also interested in exploring views about the route(s) of modern human expansions across Asia and how humans expanded to the outer extremes of the world, across Australasia, western Europe, and eventually, the New World. Another significant topic explored concerned what hominin groups were present in different areas of Asia, and what was the nature of their interactions with modern humans moving in for the first time (e.g., extinction, assimilation, nonrecognition/avoidance)? Indeed, we thought it would be interesting to examine what role, if any, did a so-called modern behavioral toolkit play in facilitating the advance of modern humans throughout Asia. Ultimately, the main goal of the symposium was to evaluate the Late Pleistocene human evolutionary record of Asia based on what we thought we knew, thereby synthesizing multidisciplinary studies during discussions, while at the same time allowing us to think about how to move the discipline forward. We review each of these themes briefly here.

In Brief: What Do We Think We Know?

The field of human evolution is currently largely focused on various models that explain the emergence, exodus, and interbreeding of our species out of Africa and into Asia, particularly various iterations of the Out of Africa 2 and Assimilation models. Based on data from several different fields, and at the time of the Sintra symposium in March 2016, most practitioners support the following points for both of these models. Modern humans first appear in East Africa sometime between 195–160 ka (McDougall et al. 2005; White et al. 2003), based on fossil and geochronological evidence and supported by early analyses of global human mtDNA sequence variation (Vigilant et al. 1991) and subsequent studies on genetic diversity and population substructure in Africa (for an overview, see Tishkoff et al. 2009). Since the time of the symposium, fossil discoveries have been published to suggest that early modern *Homo sapiens* was present across Africa by 315 ka (Hublin et al. 2017; Richter et al. 2017), suggesting an even greater complexity and possible population structure within the African continent itself. As conventional thinking goes, at around 120–100 ka, modern humans expanded into the Levant where they survived until ca. 70 ka (Grün and Stringer 1991; but see Millard 2008 for slightly younger end estimates). Most Out of Africa 2 proponents have argued that this earlier appearance of modern humans outside of Africa represents an initial failed dispersal event. It was not until well after the Toba super-eruption (~74 ka)

that a single dispersal wave out of Africa occurred, usually estimated to be around 60–50 ka (Kaifu, Izuhou, and Goebel 2015; Stoneking and Krause 2011). Some proponents of the single and late wave hypothesis argue that the dispersal event was rapid and moved along the coast of southern Asia and Southeast Asia, eventually reaching Australasia (Macaulay et al. 2005; Mellars 2006a; Oppenheimer 2009).

Proponents of the Assimilation model suggest that admixture occurred in multiple places during multiple events (Denell and Petraglia 2012; Smith et al. 1989, 2017; Trinkaus 2005). Although not necessarily one of the core criteria of the Assimilation model, it may be implied that multiple dispersals out of Africa occurred, starting during the early part of the Late Pleistocene. One of the primary fossils to support the argument for an earlier dispersal/hybridization event is the partial mandible from Zhirendong, southern China, that dates to ~113–100 ka (Liu et al. 2010a) or more recently to ~110–106 ka (Cai et al. 2017). Further reports of early modern humans from China (Lunadong, Huanglongdong, and perhaps Fuyandong) also support this scenario. The Assimilation model does not necessarily promote a particular direction for human dispersals and admixture events. Genetic studies published since 2010 have clearly indicated some level of admixture between the various hominin populations that were present in Asia during the Late Pleistocene (Curat and Excoffier 2011; Kuhlwilm et al. 2016).

In addition to human biology, the spread of so-called modern human behaviors during the Late Pleistocene appears to have occurred initially over northern Asia and then southward. An absence of what may be considered one of the core pieces of evidence of modern human behavior, blade and microblade technology in Southeast Asia, including southern China, suggests that these behaviors may have stopped someplace in central China (Norton and Jin 2009). However, given the direct evidence for early rock art in Sulawesi around 40 ka (Aubert et al. 2014) and indirect evidence of boating/rafting technology to arrive at Callao in the Philippines at approximately 67 ka (Mijares et al. 2010) and Australia between 60 and 50 ka at Madjedbebe (Clarkson et al. 2015), several lines of evidence suggest that modern humans were in the region at a relatively early date.

Topics Discussed in Sintra

The symposium was convened with many active Asia specialists in attendance, and thus we hoped to gain new insights about the occupation history of the continent. Each presentation was followed by detailed discussion about the specific paper and related topics generally. A great advantage of the symposium composition was that, for the most part, the participants brought their own primary data to the table for discussion. Although there was little clear-cut, unanimous support for any of the primary questions proposed at the outset of the symposium, as evidenced from the discussions and follow-up papers found in this volume, many authors altered their views on various subjects in light of new data and hearing opinions from other

participants. Below we discuss themes emerging from the papers, outlining information about archaeology, hominin paleontology, geochronology, and genetics.

Laying the Foundation: Contributions from Archaeology

The archaeological record serves as a fundamental backdrop on which all models project. As Bretzke and Conard (2017) justifiably note, the relative paucity of hominin fossils and consequently ancient DNA from across large expanses of the Asian continent make it difficult to generate robust models for hominin dispersal patterns and interactions. Data for such modeling can be collected, however, from large-scale archaeological survey and excavation projects. A number of archaeology-oriented papers in this volume provide the critical necessary footing to contribute to such models currently being debated: Bretzke and Conard (2017) cover Southwest Asia; Buzhilova, Derevianko, and Shunkov (2017) discuss Central Asia; Graf and Buvit (2017) review Siberia; Blinkhorn and Petraglia (2017) cover the Indian subcontinent; Wang (2017) reviews China; and Nakazawa (2017) discusses Japan. In addition, more general reviews of the East Asian record are provided by Bae (2017) and O'Connor and colleagues (2017) for island Southeast Asia. All of the authors examine the nature of regional records, while at the same time discussing their data with respect to broader topics such as the timing and route of modern human dispersals.

Dennell (2017) lays the foundation for understanding paleoenvironmental variation across Asia during the Late Pleistocene. Knowledge of the paleoenvironment is, in fact, one of the underlying themes in many of the archaeology papers because of the importance of hominin behavioral adaptations in the face of environmental variations (e.g., temperature, altitude, latitude, bathymetry). Climate change and sea level fluctuations also have consequences, as barriers may have risen up and subsequently disappeared (see also, especially, O'Connor et al. 2017, and to some extent Bae 2017; Bretzke and Conard 2017). Obviously, paleoenvironmental factors would have impacted behaviors such as subsistence strategies, tool production, and landscape movements.

Although one must be wary of drawing arrows when illustrating the direction and mode of human movement across Asia, such demonstrations do at least allow us to generate a general idea of dispersal patterns. The variations on the Out of Africa 2 and Assimilation models both agree that modern humans dispersed out of Africa and initially arrived in Southwest Asia. Based on the regional archaeology survey papers presented here, it would seem there is support for an initial movement of humans through South Asia, possibly arriving in southern China by marine isotope stage (MIS) 5 and/or 4. This is supported by hominin fossil sites such as Zhirendong, Lunadong, Huanglongdong, and Fuyandong (Bae et al. 2014; Liu et al. 2010b, 2015; but see Michel et al. 2016) and indirectly by archaeological sites from India like Jwalapuram with Middle Stone Age-like stone tool industries (Petraglia et al. 2007).

Based on current data, no sites associated with modern humans have been found in northern Asia and/or Siberia that date to MIS 5 or 4 (Buzhilova, Derevianko and Shunkov 2017; Graf and Buvit 2017). No sites in Europe currently exist that are clearly assigned to modern humans that date to these marine isotope stages either (Higham et al. 2014). This is despite the finding from a recent paleoclimate modeling study (Timmermann and Friedrich 2016) that a climate corridor may have been present between 90 and 80 ka that could have allowed modern humans to move from Southwest Asia into Europe. Accordingly, it might be argued that modern humans initially moved through South Asia and arrived in Southeast Asia before the advent of MIS 3 (Boivin et al. 2013; Petraglia et al. 2010). A second later dispersal then occurred northward, eventually reaching Siberia, that originated either in Southwest Asia or, less likely, as some earlier genetics studies suggested (e.g., Jin and Su 2000), from southern China.

A third underlying theme among the archaeology-centered papers is the role of so-called modern human behaviors in successful and unsuccessful dispersals by modern *Homo sapiens* across Asia. In particular, it is fairly clear that a set of novel behaviors accompanied, and perhaps facilitated, colonizations of regions like the Japanese archipelago and island Southeast Asia (Bae 2017; Nakazawa 2017; O'Connor et al. 2017). Some of these behaviors may have included different functional uses of ground stone tools like axes and the independent development of equipment for fishing. Further, as Bae (2017) notes in this volume, it may be possible that different ecological constraints caused the disappearance of blade/microblade technology when modern humans were moving into Southeast Asia from either South and/or North Asia (see also Bar-Yosef et al. 2012). If so, what does this say about humans' ability to adapt to new environments? Surely if they were able to produce rock art in Sulawesi by 40 ka (Aubert, Brumm, and Taçon 2017; Aubert et al. 2014) and were capable of pelagic deep sea hunting around the same time (O'Connor et al. 2011), humans in the region were clearly remarkably adaptive. The ability for modern humans to adapt well in southern Asia is clearly evident from the detailed studies of Sri Lanka's early rainforest habitation (Roberts et al. 2015) and the occupation of Niah Cave in Borneo (Barker et al. 2007). Although local extinction events may have occurred, the presence of modern humans in Southeast Asia appears fairly continuous for the past 40 ka at least.

What Do the Fossils Say?

Understanding the nature of the variation in the hominin fossil record is critical to developing ancestor-descendant or sister-sister relationship models between different hominin populations. A range of species appear to be present in Late Pleistocene Asia, namely modern *Homo sapiens*, *Homo neanderthalensis*, *Homo floresiensis*, Denisovans, and perhaps late-appearing *Homo erectus* and/or mid-Pleistocene *Homo*. Here, Kaifu (2017) and Martín-Torres et al. (2017) provide useful reviews of the Asian hominin fossil records, the former covering the earlier

periods until the late Middle Pleistocene, while the latter paper details the Late Pleistocene hominin fossil record from China. Buzhilova, Derevianko, and Shunkov (2017) and Demeter et al. (2017) contribute detailed discussions of the important fossils from Central Asia (Teshik Tash, Uzbekistan), Siberia (Denisova and other caves, Russia), and Tam Pa Ling (Laos), particularly in their broader settings.

Kaifu (2017) discusses the relationships between the different *H. erectus* populations from China and Indonesia and determines that a great deal of variation exists. Interestingly, Kaifu (2017) finds that *H. erectus* populations geographically juxtaposed between Zhoukoudian and Indonesia (e.g., Yunxian, Hexian, Yiyuan, Tangshan) do not simply display gradational variation between the two regions and may in fact represent a previously unidentified third *H. erectus* population. Kaifu (2017) also reviews the “late archaic *Homo*” record from eastern Asia. It should be noted that some authors refer to these fossils as “mid-Pleistocene *Homo*” given the nomenclatural baggage with assigning the word “archaic” to a taxonomic group (for various discussions, see Bae 2010; Tattersall 1986; Tattersall and Schwartz 2008; Xiao et al. 2014).

A question that was raised during the symposium included whether mid-Pleistocene *Homo* from China are the fossilized remains of the Denisovans. This idea was broached when it was fairly evident that the Denisovan and Xujiayao hominin molars are both extraordinarily large. Here, Martínón-Torres et al. (2017) also suggest that Denisovans may already be present skeletally in China in the form of the Xujiayao and/or Maba fossils or perhaps a yet to be identified hominin population (e.g., Penghu 1 from Taiwan). Since the conference, Smith et al. (2017) raised the same question, and a nonmetric analysis of the Denisova and Xujiayao teeth found several similarities (Zubova, Chikisheva, and Shunkov 2017). Further, Kaifu (2017) suggested late *H. erectus* from Indonesia may be the ancestral population of the Denisovans given their apparent presence in modern populations of island Southeast Asia. This would imply that a subpopulation of Denisovans later dispersed north to Siberia or that Denisova simply represents the northern edge of the distribution of this group. Interestingly, Zubova and colleagues (2017) found nonmetric similarities between the Denisovan and Sangiran *H. erectus* fossils from Indonesia as well. However, Buzhilova, Derevianko, and Shunkov (2017) found metric and morphological similarities between the Denisovan, Teshik-Tash, and Oase 2 dentition, suggesting gene flow between Europe and Siberia. The Teshik-Tash hominin fossils are generally assigned to *H. neanderthalensis* (Gremyatskii 1949; Krause et al. 2007), while Oase 2 is considered an early modern human (Trinkaus et al. 2003). We are intrigued by the possibility that Denisovans may already be present in the skeletal record in the form of *H. erectus*, Chinese mid-Pleistocene *Homo*, Teshik-Tash Neanderthals, early modern humans, or a yet to be determined ghost lineage. We hope future research is directed to test this hypothesis.

Another interesting point raised by Martínón-Torres et al. (2017) is the possibility that some of the morphological anom-

alies from *H. floresiensis* (e.g., rotated P4s, unique p3) may actually be the result of introgression between different hominin populations. The appearance of such anomalous traits could also be the result of inbreeding, but examples from Rebecca Ackermann’s research on hybrids in nonhuman primates (e.g., Ackermann 2010; Ackermann, Rogers, and Cheverud 2006) does suggest this could be an alternative hypothesis that needs to be tested. If it turns out that Martínón-Torres et al. (2017) are correct, then *H. floresiensis* may not have lived in total isolation for more than a half-million years, as many studies suggest.

In addition to previous studies that argue for a pre-60 ka presence of modern *H. sapiens* in eastern Asia (e.g., Bae et al. 2014; Liu et al. 2010a, 2010b; Mijares et al. 2010; Norton and Jin 2009; Shen et al. 2002), Liu et al. (2015), Martínón-Torres et al. (2017), and Demeter et al. (2012, 2017) strongly promote Fuyan Cave (China) and Tam Pa Ling (Laos) as additional evidence for an early appearance of modern humans in the region. With the increasing hominin fossil record from the region, perhaps this should not come as that much of a surprise, as almost 1 decade ago Norton and Jin (2009:258) noted that “growing evidence suggests that modern humans may have been present in East Asia before ~50 kya.” Although questions still need to be resolved about the dating schematic for Fuyan Cave (see Michel et al. 2016), the Tam Pa Ling evidence seems to be fairly robust as an early example of modern humans in the region by at least ~70 ka. If any, or all, of these sites (Luna, Huanglong, Fuyan, Tam Pa Ling, Callao Cave) can stand up to further scientific scrutiny, then any continued argument that dispersal by modern humans out of Africa did not occur until after 60 ka can be shelved. Needless to say, it is clear that geochronology plays a critical role in determining the importance (or nonimportance) of many of these proposed early sites.

The Importance of Geochronology

Besides the discovery of hominin fossils and archaeological sites, one of the most important questions that needs to be answered is how old the site and the materials are. In the past decade, extensive work in other parts of the world, namely Europe and Africa, have revealed significant discrepancies between previous chronologies and renewed dating attempts. For example, at over 100 Paleolithic sites (re)examined by the Oxford radiocarbon lab since 2006, as much as 70% of the previous dates were erroneous (Higham 2011). This has led to renewed discussion on the date and nature of Neanderthal extinction and the timing, tempo, and pathways of modern human expansion as well as the possible overlap of the two human species within Europe and the Near East (see, e.g., Mellars 2005, 2006a; Zilhão 2006; Zilhão and d’Errico 1999). The new radiocarbon chronologies, augmented with better statistical (Bayesian) methods, have already clarified aspects of many of these debates in Europe (e.g., see Higham et al. 2014 for the timing of the extinction of Neanderthals in Europe). Similarly in Africa, new dating programs mainly using luminescence dating and in particular, single-grain OSL (optically stimulated lumines-

cence), have elucidated long-debated issues such as the age and final manifestations of the Aterian and other Middle Stone Age facies both in the north, east, and south of the continent (e.g., Douka et al. 2014; Gliganic et al. 2012; Jacobs et al. 2008a, 2008b, 2012). In Asia a reliable chronological framework for the vast majority of its subregions is still lacking, although systematic application of such methodologies on a number of Asian sites is currently underway.

The two geochronology contributions to the symposium focus on major innovations and improvements to ^{14}C and uranium-series dating methodologies and how these methodological advances can contribute to a better understanding of the Late Pleistocene Asian paleoanthropological record (Aubert, Brumm, and Taçon 2017; Douka and Higham 2017). Aubert and colleagues (2017) describe the U-series dating of a new series of sites from Sulawesi in Southeast Asia, while Douka and Higham (2017) discuss the results of redating of important sites from Georgia and Russia (Bondi Cave and Kostenki 14). Douka and Higham (2017) note that improved methods and the capability to incorporate various chronometric and paleoclimatic data into single-site regional and multiregional Bayesian models offer unique glimpses into human evolutionary pathways. Importantly, both papers (Aubert, Brumm, and Taçon 2017; Douka and Higham 2017) emphasize strongly the importance of using a combination of dating techniques and multiple dates from the same layers to narrow the age bracket of various sites. A good example that appears in this volume is Demeter et al. (2017), which presents a new human fossil from the lowest stratigraphic layer at Tam Pa Ling, almost 6 m below the surface, that was dated by a combination of methods to possibly as old as ~70 ka.

And the Genetics Say?

One area of research that is playing an increasingly important role in the Out of Africa debate is paleogenetics. Many genetic studies focus on analyzing ancient DNA from human fossils, while a good number of studies evaluate modern genetic data (e.g., mtDNA, Y-chromosome) to work backward in time. In both types of studies, data are used to reconstruct the timing of population extinctions and divergences and the degree of introgression between different populations. For instance, many genetic research teams are currently trying to determine the extent of the Denisovan distribution throughout Asia, particularly Southeast Asia, as reconstructed from various population genetic models. The Sikora (2017) contribution here is a review of the major genetic studies that focus on the Asian Late Pleistocene record. Interestingly, Sikora (2017) draws the conclusion “that failed dispersals and large-scale population replacements and admixture, as well as repeated colonization of geographic regions, were likely the norm rather than the exception throughout much of human history.” Although not focused on genetic modeling, Reyes-Centeno et al. (2017) use dental nonmetric data to test various modern human dispersal models (single vs. multiple), many of which have

their foundation within genetic research. Sikora (2017) and Reyes-Centeno et al. (2017) both emphasize taking a careful approach to these genetic studies and that different methodologies may not properly map population histories correctly. For instance, relying solely on modern genetic data does not allow confident estimates of when two populations initially diverged, especially given the uncertainties surrounding variation in mutation rates (Scally and Durbin 2012; Sikora 2017).

Where Do We Go from Here?

At the conclusion of the symposium, we were unable to draw any unanimous conclusions to many of the questions that were posed. In some respects, we see this as a success and as an opportunity. The intent of the symposium was to bring in scientists from different disciplinary backgrounds to evaluate key questions and determine if there was a consensus after scientific scrutiny, particularly when viewed from multidisciplinary perspectives. Although none of the topics were entirely agreed upon, some did fare better than others. For example, one important conclusion drawn from the symposium and this resulting volume is that the dispersal out of Africa and into Asia should not be seen as a single unidirectional event but, rather, as a series of multiple dispersals in a multitude of geographic directions; such movements, and their tempo and relative success, were at least in part influenced by environmental factors (deserts, mountain ranges, reliable water sources, fluctuating bathymetry, etc.). However, since the symposium, a set of genetics papers was published in *Nature* (Malaspinas et al. 2016; Mallick et al. 2016; Pagani et al. 2016). They conclude that the primary human expansion out of Africa and across Asia occurred around 60 ka. Even among these recent papers, though, the Pagani et al. (2016) study differs in that Pagani and colleagues suggest that traces of earlier human dispersals in the modern gene pool, possibly as early as 100 ka, are present in modern-day Papuan populations. What is not yet clear from these studies is whether the origin of *Homo sapiens* is much older in Africa (Hublin et al. 2017) than estimated by most genetic clocks and whether we can thus suggest an earlier movement of modern humans out of Africa.

There are new testable hypotheses that were raised in Sintra and in the set of articles included in this special issue that will likely influence the future direction of human evolutionary studies in Late Pleistocene Asia. For instance, the question arises as to whether the Denisovans are already known and present in eastern Asia in the form of Chinese mid-Pleistocene *Homo*. The data appear to be already available to test this hypothesis, but this would need to be evaluated further. We can also ask the question as to whether available data support or refute single or multiple dispersal models and whether there was a pre- or post-Toba eruption appearance in the region. The detailed archaeology reviews of each of these different regions should allow us to be better able to connect the dots, so to speak, regarding the frequency, direction, and timing of dispersal patterns of modern humans and other populations.

More rigorous geochronological evaluations are only helping us to develop more robust models. Genetic studies will continue to force paleoanthropologists to rethink their data and models when certain “ghost” lineages appear.

All participants in the symposium agreed that more data are critical to addressing evolutionary and biogeographic questions, particularly from regions that have been subjected to less intensive multidisciplinary paleoanthropological research (e.g., Central and Southeast Asia). In line with this, we need to delve more deeply into the better-known records from places like China and the Indian subcontinent because, even there, there are vast pockets of largely unexplored areas from a fieldwork perspective. The diversity of interesting and important findings coming out of Asia on an annual, monthly, or even weekly basis argues strongly for the importance of the continued development of large-scale interdisciplinary research approaches to just about all regions of Asia.

The origin of modern humans will continue to be of enormous interest to both the public and the scientific community. As attested to by the various papers in this volume, there are a great deal of significant data coming out of Asia that are not only of public interest but are helping to turn the field on its head. Moving forward, we hope that this special issue serves to lay the foundation for an increase in multidisciplinary research in Asia focused on this topic. We are confident that this will lead not only to many additional important findings but also to the improvement and development of more robust models to explain the nature and timing of modern human dispersals across Asia and beyond. We hope that this special issue of *Current Anthropology* serves to encourage future generations of students interested in the origin and evolution of our species to pick up this baton.

Acknowledgments

We are grateful to the Wenner-Gren Foundation for providing the funding to hold the week-long symposium in Sintra, Portugal, in a rather beautiful hotel tucked away in the mountains. We thank Leslie Aiello for her support and guidance from our initial application. We acknowledge Laurie Obbink’s herculean organizational efforts that made the symposium a happy and extremely successful event. Leslie and Laurie’s support from the early stages of this project in the fall of 2014 to the symposium itself in March 2016, and then finally through to the *Current Anthropology* volume, were paramount to making this such a smooth process. Our conversations in Sintra were enriched by the insights and general assistance of our conference monitor and colleague, Patrick Roberts. We also wish to thank the symposium participants who came from many different places around the world. The week-long meeting led to various discussions during the sessions, meals, and breaks that really contributed to a better understanding of Late Pleistocene human evolution in Asia, particularly by being able to hear other researchers’ perspectives on the same topics. We believe that

many positive outcomes developed and will develop from this meeting. For that, we sincerely appreciate the camaraderie of the group.

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